The gibbon's Achilles tendon revisited: consequences for the evolution of the great apes?

Aerts, Peter; Thorpe, Susannah; D'Août, K; Berillon, Gilles; Vereecke, EE

DOI:
10.1098/rspb.2018.0859

Document Version
Peer reviewed version

Citation for published version (Harvard):
Aerts, P, Thorpe, S, D'Août, K, Berillon, G & Vereecke, EE 2018, 'The gibbon's Achilles tendon revisited: consequences for the evolution of the great apes?', *Royal Society of London. Proceedings B. Biological Sciences*, vol. 285, no. 1880, 20180859. https://doi.org/10.1098/rspb.2018.0859

The gibbon's Achilles tendon revisited: consequences for the evolution of the great apes?

Peter Aerts [1,2], Kristiaan D'Août [3, 1], Susannah Thorpe [4], Gilles Berillon [5] and Evie Vereecke [6]

[1]: Department Biology, University of Antwerp (BE)
[2]: Department of Movement and Sports Sciences, University of Ghent (BE)
[3]: Department of Musculoskeletal Biology, University of Liverpool (UK)
[4]: School of Biosciences, University of Birmingham (UK)
[5]: Department of Prehistory, MNHN, CNRS (FR)
[6]: Department of Development and Regeneration, University of Leuven (BE)

Corresponding Author:
Peter Aerts
FunMorph-lab
Department of Biology
University of Antwerp (CDE)
Universiteitsplein 1
B2610 Wilrijk
Belgium
peter.aerts@uantwerpen.be

Abstract

The well-developed Achilles tendon in humans is generally interpreted as an adaptation for mechanical energy storage and reuse during cyclic locomotion. All other extant great apes have a short tendon and long-fibered triceps surae, which is thought to be beneficial for locomotion in a complex arboreal habitat as this morphology enables a large range of motion. Surprisingly, highly arboreal gibbons show a more human-like triceps surae with a long Achilles tendon. Evidence for a spring-like function similar to humans is not conclusive.

We revisit and integrate our anatomical and biomechanical data to calculate the energy that can be recovered from the recoiling Achilles tendon during ankle plantar flexion in bipedal gibbons. Only 7.5% of the required external positive work in a stride can come from tendon recoil, yet it is delivered at an instant when the whole body energy level drops. Consequently, an additional similar amount of mechanical energy must simultaneously dissipate elsewhere in the system. Altogether, this challenges the concept of an energy-saving function in the gibbon's Achilles tendon.

Cercopithecids, sister group of the apes, also have a human-like triceps surae. Therefore, a well-developed Achilles tendon, present in the last common 'Cercopithecoidea-Hominoidea' ancestor, seems plausible. If so, the gibbon's anatomy represents an evolutionary relict ('no harm – no benefit'), and the large Achilles tendon is not the premised key-adaptation in humans (although the spring-like function may have further improved during evolution). Moreover, the triceps surae anatomy of extant non-human great apes must be a convergence, related to muscle control and range of motion. This perspective accords with the suggestions put forward in the literature that the last common hominoid ancestor was not necessarily great-ape-like, but might have been more similar to the small-bodied catarrhines.

State of the art

When looking at the gross morphology of the triceps surae in the extant great apes[1], the difference between humans and the other species is conspicuous (Fig1). In humans, the bellies of the gastrocnemius muscle are short-fibered and pennate, and insert together with the soleus via a well-developed Achilles tendon onto the calcaneus (e.g. Frey, 1913; Swindler and Wood, 1973; Standring, 2016). In contrast, in non-human great apes, an Achilles tendon is externally barely visible and the bellies of the gastrocnemius muscle are extended with a more parallel orientation of the long muscle fibres (e.g. Frey, 1913; Hanna and Schmitt, 2011; Swindler and Wood, 1973; Thorpe et al, 1999; Vereecke et al., 2005a; Myatt et al, 2011). These contrasting morphologies correlate with differences in locomotor repertoire: while orangutans, gorillas, chimpanzees and bonobos share a wide range of, often arboreal, locomotor behaviours such as orthograde (i.e. upright trunk) suspension and clambering, quadrupedalism, vertical climbing and hand-assisted bipedalism (see Thorpe and Crompton, 2006 and Hunt, 2016 for reviews), modern humans are primarily terrestrial habitual bipeds.

The well-developed human's Achilles tendon is considered to be an adaptation for energy-efficient cyclic locomotion and is assumed to have originated at some point after 3 million years (Myr) ago in the genus *Homo* (Bramble and Lieberman, 2004). The tendon is stretched and loaded with strain energy during initial dorsiflexion (decreasing ankle angle) of the stance phase and recoils during the plantar flexion (increasing ankle angle) later in stance to power the foot push-off. As such, the Achilles tendon is a component of the spring element in the SLIP-mechanism (Spring Loaded Inverted Pendulum; Full and Koditschek, 1999; Geyer et al., 2006) that is optimally functioning during running: the kinetic and potential energy that must be extracted from the system at the whole body level early in stance (the so-called negative external work) is converted - at least partly - to strain energy in the spring element and this is recycled to power part of the subsequent push off (e.g. Alexander, 2003; Bertram, 2016). In humans, at a running speed of 4.5 ms^{-1}, 35% of the required external positive work per stride can thus be recovered from the recoil of the Achilles tendon (e.g. Alexander, 1991, 2003).

The morphology of the non-human great apes, on the other hand, is generally considered to represent the ancestral state (Bramble and Lieberman, 2004), being beneficial when moving about in an arboreal environment. Movement patterns are less cyclic and less uniform and the long-fibered muscles facilitate muscular control over a large range of motion, which is essential to deal efficiently with the high 3-dimensional complexity of the habitat and to respond to the compliance of the substrate (Myatt et al., 2011; Preuschoft et al., 1992; Thorpe et al., 1999).

Remarkably, given their phylogenetic position and their largely arboreal lifestyle, the gibbon's triceps surae has a more human-like appearance (Fig1). There is a long and well-developed Achilles tendon, firmly attaching onto the heel bone, and the muscle bellies of the gastrocnemius are short-fibered and pennate (Frey, 1913; Vereecke et al., 2005a). Questioning the adaptive meaning of this morphology in the primarily brachiating lesser apes seems essential to understand the evolution of locomotor diversity in the apes.

Because of the high resemblance between the gibbon and human Achilles tendon, it is tempting to search for an explanation for gibbons that follows a similar line of thought to that assumed for the human Achilles tendon. When on the ground to cross gaps between trees that are too large to cross arboreally, or when moving on large tree branches, gibbons most often use a bipedal gait (Vereecke et al., 2006a; Baldwin and Teleki, 1976; Fleagle, 1976; Gittins, 1983; Sati and Alfred, 2002). Despite

[1] Here, orangutans, gorillas, chimpanzees, bonobos *and* humans are considered the extant great apes (i.e. extant Hominidae).

the presence of a double support phase (i.e. both feet on the ground simultaneously; there is no aerial phase in the bipedal cycle), this gait must be classified as 'grounded running' (cf. Vereecke et al., 2006b,c) as is also found for terrestrial locomotion in birds (e.g. Andrada et al., 2013, 2015): at the whole body level, kinetic and potential energy fluctuations accord to the dynamics of running (i.e. in-phase decrease and subsequent increase of kinetic and potential energy in each single step; Vereecke et al., 2006b, Vereecke & Aerts, 2008). As such, the SLIP-mechanism might be functional. Moreover, the safety factor of the Achilles tendon (i.e. tendon strength over tendon loading) appears, together with that of the patella tendon, to be the lowest of all the hind limb muscles in the gibbon (Vereecke et al., 2005a; Channon et al., 2009; Vereecke and Channon, 2013). A low (but safe) safety factor is required for functionally significant energy storage and recoil. Furthermore, the ratio of the tendon length over the effective muscle fascicle length (i.e. accounting for pennation angle) is rather high for the triceps surae (Vereecke et al., 2005a; Channon et al., 2009; Vereecke & Channon, 2013). Such muscle-tendon morphology can be expected if the tendon needs to do the work. One may also look at this from a slightly different perspective. Channon et al. (2009) presented the relationship between the physiological cross-sectional area (PCSA; measure for potential maximal load) of the limb muscles and their fascicle length (measure for the potential shortening), thus representing a sort of concentric work space, as it expresses the potential maximal load against potential shortening. Muscle-tendon-complexes that are part of the spring-element of the SLIP-mechanism should combine a high PCSA or force output with short fibres, enabling the tendon to do most of the concentric work. Surprisingly, all plantar flexors occupy a rather 'unspecialized' region in the concentric work space where small PCSA and short fibres are combined (see Channon et al., 2009). In this respect, gibbons appear to be no different from the non-human great apes.

The role of the tendon revisited

The evidence provided above for the gibbon's Achilles tendon working as energy-saving device during 'grounded' running is indirect. Moreover, its identification as 'unspecialized' in the muscle-tendon workspace could be interpreted as a counter-indication for this role and former analyses (Vereecke et al., 2006b; Vereecke and Aerts, 2008) were also unable to categorically demonstrate an energy-saving role during grounded running. Here we take a novel approach to resolve this debate. The amount of strain energy that is stored *in vivo* in the tendon of the white-handed gibbon (*Hylobates lar)* during walking steps at the onset of plantar flexion, and that can thus potentially be recovered via recoil, is calculated and compared with the mechanical work input needed at the whole body level (the so-called positive external work) to complete a walking cycle (i.e. stride = left + right step). In order to do so, the kinematic, dynamic, material property and anatomical data collected by Vereecke et al. (2005a,b, 2006a,b,c), Vereecke and Aerts (2008), Channon et al. (2009, 2010b) and Vereecke and Channon (2013) will be combined in a new synthesis. (A short synopsis of the Materials and Methods of these papers is included as supplementary material).

When the Centre Of Pressure [COP; instantaneous position of the point of application of the resultant Ground Reaction Force (GRF) at the plantar surface of the foot] is known throughout the ground contact phase, the moment of the GRF with respect to the ankle joint can be determined quite accurately as a function of stance time by multiplying at any instant the GRF with the perpendicular distance from the joint centre to the GRF (Fig2A) [2]. This moment (dashed curve) is presented together with the ankle joint kinematics (thin curve) as a function of normalized stance time in Fig2B. For the

[2] Inertial effects can safely be neglected in this account, given the small mass (1.2% of total body mass) and the low accelerations of the slender foot segments (cf. Vereecke et al., 2006b; Vereecke and Aerts, 2008).

larger part of stance (about 79%), the ankle joint dorsiflexes and only during the last 21% of stance, does it plantar flex again, to power the foot push-off. At the onset of plantar flexion, the (minimal) ankle joint angle reaches 103° and the *in vivo* moment of the GRF that tends to dorsiflex the joint equals 2.60 Nm (see Fig2B).

At any instant in the stride, the moment of the GRF with respect to the ankle must be balanced by the muscle-tendon-systems that cross the joint. It is therefore possible to estimate the *in vivo* tensile force acting along the Achilles tendon at the onset of ankle plantar flexion, provided that the moment arm of the Achilles tendon (i.e. perpendicular distance from the joint centre to the tendon; Fig2A) at the coinciding joint angle (103°) is known [3,4]. Muscle moment arms were accurately determined by Channon et al. (2010b). For an ankle joint of 103°, the moment arm of the Achilles tendon in *Hylobates lar* recalculates to 1.48 cm. Consequently, the *in vivo* tensile force along the tendon at the onset of ankle plantar flexion equals 175.67 N [i.e. 2.60 Nm/(1.48 cm 10^{-2})].

Cyclic tensile load-deformation tests on the Achilles tendon were carried out by Vereecke and Channon (2013). The tendon's behaviour conforms to that of the text book examples (e.g. Alexander, 2003): apart from a toe-region at low loads, the load-deformation relationship is rather linear at higher loading; at recoil, a hysteresis of on average 13.5% (mean $\pm$ SD = 3.4%; n=14) is observed (i.e. difference between loading and unloading energy). The slope of the linear loading part gives the stiffness, which is on average 99.6 Nmm^{-1} (mean $\pm$ SD = 42.7 Nmm-1; n=14). Since the tensile force divided by the stiffness equals the extension of the tendon, the *in vivo* stretch of the Achilles tendon at the onset of the ankle plantar flexion amounts to 1.76 mm (i.e. 175.67 N/99.6 Nmm^{-1}).

Finally, the amount of strain energy that is stored in the Achilles tendon at the onset of ankle plantar flexion (and which is available to power the plantar flexion) is represented by the area under the load-deformation curve. Because of the largely linear behaviour when loaded, this area is given by (175.67 N x 1.76 mm 10^{-3})/2 which equals 0.15 J.

At the whole-body level, the positive work needed to complete a stride amounts on average to 3.56 J (Vereecke et al., 2006b)[5]. Taking the 13.5% hysteresis into account, 0.26 J [i.e. (0.15 J left + 0.15 J right) x (1-0.135)] of this can theoretically be recovered from the recoiling left and right Achilles tendons during the push-off of the feet. This amounts to merely 7.5% of the required external positive work per stride. This amount can directly be compared with the 35% mentioned above for humans (but see also [6]). More importantly, however, plantar flexion seems to come at the wrong instant. To be

[3] In this approach is assumed that the balancing activity is taken entirely by the triceps surae, hence solely acting along the Achilles tendon. As such, the estimate for the tensile force along the tendon at the onset of ankle plantar flexion represents a maximal estimate, as co-contraction of the digital flexors would result in a reduction of the Achilles tendon stress.

[4] It should be noted that co-contraction of the dorsiflexors (which could lead to higher tensile stress in the Achilles tendon) at that instant in stance is highly unlikely.

[5] This must be considered as a minimuml estimated for the required positive work input, as this concerns the external work only (i.e. whole body level; movements of the Body Centre Of Mass or BCOM). Swinging the limbs with respect to the BCOM can represent a considerable extra cost (see for instance Marsh et al., 2004).

[6] Similar approaches on human running (4.5 ms^{-1}) show 35% of the external positive work (mechanical energy) comes from elastic recoil of the Achilles tendon during the second half of the ground contact phase in each cycle; i.e. energy stored during the first half of stance (Ker et al., 1987, Alexander, 1991, 2003). This is probably even a conservative estimate. Lai et al. (2014) show that at comparable running speeds, energy recovery from the triceps surae tendon can amount to more than 50J per step (which is about 140% of what was determined from the former ex-vivo experiments; see Lai et al., 2014 and references therein). Clearly, the eccentric-concentric work of the triceps surae during running steps will still require metabolic energy, even when the entire strain cycle of the muscle tendon unit (MTU) is taken by the tendon. Cross-bridge cycling is needed to prevent extension of the muscle belly and enable loading of the tendon (e.g. Fletcher and MacIntosh, 2015).

effective, tendon recoil should happen when the mechanical whole body energy level increases (i.e. mechanical energy is added to the system). However, most often (step-to-step variability is observed) plantar flexion just occurs when, at the whole body level, mechanical energy must be extracted from the system (i.e. negative work must be performed; Fig2B). Consequently, Achilles tendon recoil in plantar flexion during ground contact (which means that mechanical energy is added to the system) could eventually come at the extra cost for energy dissipation by eccentric muscle contraction. Moreover, the foot is only partially plantar flexed at the end of stance when the joint torque is zero again (Fig2B). This means that either the recoil energy is dissipated by extending the triceps surae muscle belly during that final stance phase or, because of the biarticular arrangement of the gastrocnemius, that energy is transferred to the knee to assist further active knee flexion observed final in stance (see Vereecke et al., 2006b)[7].

If not for energy storage and recoil during grounded running locomotion, what could the explanation of the well-developed Achilles tendon in gibbons be? Clearly, other, even rare behaviours may entail selective pressure and morphological adaptation. Gibbons also engage, for instance, in bipedal and tripedal gallops and a sort of half bound (crutching gallop) (cf. Vereecke et al., 2006a), and show excellent leaping performance. The potential use of tendon recoil for energy recovery (while galloping) or power amplification (for leaping) cannot be excluded, but biomechanical results presented by Channon et al. (2010a, 2011a,b) do not support this for leaping.

Here, we propose an alternative perspective. Available information from the literature and our own observations suggest that the Achilles tendon is also well-developed and firmly attaching to the heel bone in extant Cercopithecoidea (e.g. Frey, 1913; Swindler and Wood, 1973; own dissections on *Theropithecus gelada* (gelada baboon)*, Papio anubis* (olive baboon)*, Macaca maura* (Moor macaque)*, Macaca mulatta* (rhesus monkey), *Semnopithecus entellus* (Hanuman langur), *Colobus guereza kikuyensis* (mantled guerza)*, Colobus* spec.*, Trachypithecus francoisi* (François' leaf monkey); see supplementary material and Fig1). It seems therefore conceivable that this morphological character was also present in the basal ancestor of this superfamily, hence also in the basal representative of the sister taxon, the Hominoidea (Fig1). Is it plausible that the Achilles tendon is retained as a relict in the branch leading to the Hylobatidae (Fig1)?

If selection acted predominantly on the principal locomotor mode in gibbons, i.e. on brachiation (e.g. Bertram 2004; Bertram & Chang, 2001; Bertram et al., 1999; Chang et al., 1997, 2000; Fleagle, 1976; Michilsens et al., 2011, 2012; Preuschoft & Demes, 1984; Usherwood & Bertram, 2003; Usherwood et al., 2003), adaptations can be expected primarily at the level of the forelimbs. During brachiation, hindlimb movements are potentially useful to modulate whole body rotational inertia and to avoid hitting lower lying branches, a role which, most likely, did not imply important adaptive modifications of the lower hind limb muscles. As such, it can be hypothesized that the triceps surae, with its long tendon, was not under selective pressure (no harm, no benefit) and could keep its ancestral appearance during hylobatid evolution.

For this purpose, short-fibred (pennate) bellies are the best option: these can deliver the required force at a minimal metabolic cost. At the MTU-level, in humans, up to 75% of the positive work output comes from the tendon (e.g. Hof et al., 2002; Lai et al., 2014). Given an efficiency of 0.2 – 0.25 for concentric work in muscle (Woledge et al., 1985), similar MTU stress-strain cycles for 'long-fibred – short tendon' triceps surae muscle would become very expensive.

[7] It should be noted that this conclusion refers to the role of the Achilles tendon during plantar flexion of the foot only. It may well be that other muscle-tendon systems (for instance the digital flexors or the knee extensors) do act as functional energy-saving mechanisms.

Consequence for the evolution of the great apes

If the above hypothesis is supported, then the short-fibred gastrocnemius muscle with a long Achilles tendon should also be ancestral for the Hominidae. Given that this represents also the extant human morphology, it seems most parsimonious that this ancestral morphology was retained rather than re-acquired in the evolutionary lineage leading to the habitually bipedal, terrestrial modern humans. This lends weight to Thorpe et al.'s (2007) conclusion that human bipedalism is less an innovation than an exploitation of a locomotor behaviour retained from the common great ape ancestor. To be effective, the recoiling Achilles tendon should work against a stiff lever as it is functionally present during the push-off phase in the modern human foot. Considerable evidence exists that early hominins had more mobile feet and, therefore, probably a less complete toe-off function compared to modern humans (e.g. Lieberman, 2012). Thus, although the performance of the Achilles tendon as energy-saving device might well have been further improved during human evolution[8], considering the emergence of the human Achilles tendon as a key adaptation for economical cyclic bipedal locomotion is probably no longer appropriate.

This also implies that the 'long-fibered – short tendon' appearance of the triceps surae in the orangutan, the gorilla, the chimpanzee and the bonobo does not represent the retained ancestral state as it is generally considered (cf. above). Rather, it might represent further convergent evolution from an above-branch quadrupedal ancestor (cf. Almécija et al, 2009; Alba et al., 2015) with short-fibred gastrocnemius muscles and a long Achilles tendon, towards the long-fibered muscles facilitating the muscular control and large range of motion that is beneficial for the arboreal lifestyles of each of the large-bodied extant non-human Hominidae (see for instance Myatt et al., 2011; Preuschoft et al., 1992; Thorpe et al., 1999)[9]. In this context, it is remarkable that lorisines also have a short Achilles tendon

[8] Given that modern humans gain up to 35% of the positive BCOM work required for running from tendon recoil (e.g. Alexander, 2003; about 5x more than what can potentially be recovered in gibbons), it is tempting to speculate on what has changed during human evolution to improve the percentage contribution of elastic recoil. This percentage increase may be due to (relatively) lower positive BCOM work requirements, (relatively) higher energy storage in the tendon, or both. The positive work requirements over a complete cycle (L+R) for human running at preferred speed are 3.4 J/kg (body mass; Fiers et al., 2013; Willems et al., 1995), much higher than the 0.6 J/kg here calculated for the gibbon (3.6 J/cycle for 6.3 kg animal; cf. Supplementary Material). Consequently, elevated energy storage must be in play. Human Achilles tendon stiffness is rather variable (for instance depending age or training level), but an average and physiologically relevant value of 180 Nmm^{-1} is reported in literature (e.g. Lichtwark & Wilson, 2005, 2006; Uchida et al., 2016), nearly doubling the stiffness of the gibbon's tendon. Stiffer tendons imply less elastic energy storage for a given tendon loading. Thus, tendon force at the onset of plantar flexion (enabling recoil) has to be considerably higher in humans. The ankle extension torque is maximal and equals 2.5 Nm/kg (Fiers et al., 2013; preferred running speed) when plantar flexion starts (about at midstance; notice that this value increases further with running speeds). Taking account for the according Achilles tendon moment arm of about 5 cm (e.g. Leardini & O'Connors, 2012; Maganaris et al., 2000; relative to the lower leg length about twice that of the gibbon), maximal tendon loading equals 50 N/kg , actually not that much higher than what can be calculated for the gibbon (29 N/kg = 2.6 Nm/6.3kg/0.0148m). In other words, size (body mass) as such (obviously coupled to the specific locomotor dynamics) seems to be an important determinant for the higher elastic energy storage. Using the above mentioned data for human preferred running (and accounting for an hysteresis of 10%; e.g. Fletcher & MacIntosh, 2015; Uchida et al., 2016) the relative energy storage over a cycle recalculates to 0.7J/kg which is about 17x more than in the gibbon (0.041J/kg = 0.26J/6.3kg) and accounts (at this relatively slow running speed) for 21% of the positive BCOM work.

[9] It should be noted that this alternative scenario does not necessarily imply a larger number of character-state changes (i.e. being less parsimonious) than the classical scenario in which the 'short-fibered - long tendon' triceps surae evolved independently from a 'long-fibred – short tendon' ancestral state in both the gibbons and humans. If it is agreed that the common ancestor of the cercopithecoids and hominoids shared the 'long-tendon' character state (cf. main text and see supplementary material), this feature must first have been lost,

comparable to great apes (Hanna & Schmitt, 2011) which is interpreted as a convergent feature (next to others) related to selection for slow, cautious arboreal clambering (see for instance Cartmill and Milton, 1977). This view conforms to the suggestion by Alba et al. (2015) that the last common hominoid ancestor was not necessarily great-ape-like and that small-bodied catarrhines could have played a remarkable role in ape evolution. It also accords with the suggestions by Almécija et al.(2009) (based on their analysis of hominoid forelimbs) that above-branch quadrupedalism inherited from stem hominoids constituted a significant component of the locomotor repertories of different hominoid lineages at least until the late Miocene. And finally, it also supports the suggestion by Lovejoy et al.(2009a,b) that the last common ancestor of the African apes likely had feet that functioned like those of living monkeys rather than like those of apes. Based on the present revision, it seems plausible to include the evolution of the Achilles tendon in their functional perspective, and to extend this to all extant great apes.

Ethics Statement

This paper revises and integrates previously published data. We refer to the source publications (cf. references). No additional experiments were carried out.

Data Accessibility

This paper revises and integrates previously published data. We refer to the source publications (cf. references). No additional data were collected for the purpose of this specific contribution. On request, more information can be provided by the authors (contact dr. evie.vereecke@kuleuven.be).

Funding

There is no specific funding for this contribution.

Author Contribution

PA provided the new perspective, revisited and integrated the original data, participated in some of the original data collection, participated in the final discussion and drafted the manuscript; KD participated in the collection of the original data and participated in the final discussion on the manuscript; ST brought in the evolutionary insights and participated in the final discussion on the manuscript; GB provided the anatomical data on *Macaca*, *Papio* and *Colobus* and participated in the final discussion on the manuscript; EV carried out and/or supervised all the studies providing the original data and participated in the final discussion on the manuscript. All authors gave final approval for publication.

Competing Interests

We have no competing interests.

Acknowledgements

We would like to thank the staff of the Animal Park Planckendael for access and support in studying the gibbons. We also want to acknowledge Timo Van Leeuwen for the art work in this manuscript. Part of the original studies were funded by the Research Foundation Flanders, and part of the dissections of cercopithecoids were funded by the International Research Network (IRN, CNRS) *Bipedal Equilibrium*. R. Lacoste (CNRS Primatology Station, Rousset, France). Dr. M. Herbin (National Museum of Natural History, Paris, France), Dr. François Druelle (University of Antwerp) and dr. Mélanie Berthet

in order to re-appear then in the stem hylobatids (as all seem to have a well-developed tendon) and in humans independently. This implies an identical number of character-state changes as for the premised convergent appearance of the 'long-fibred – short tendon' state of the triceps surae in the non-human great apes.

(zoo of Besançon, FR) were very helpful in collecting additional cadaver material of cercopithecoids and in assisting with the dissections.

References

Alba, D., S. Almécija, D. DeMiguel, J. Fortuny, M. Pérez de los Ríos, M. Pina, J. Robles, S. Moyà-Solà (2015) Miocene small-bodied ape from Eurasia sheds light on hominoid evolution. Science. 350: DOI: 10.1126/science.aab2625.

Almécija, S.,D Alba & S. S. Moyà-Solà (2009) Pierolapithecus and the functional morphology of Miocene ape hand phalanges: paleobiological and evolutionary implications. Journal of Human Evolution 57: 284–97.

Alexander, R.McN (1991) Energy-saving mechanisms in walking and running. Journal of Experimental Biology. 160: 55-69.

Alexander, R.McN. (2003) Principles of animal locomotion. Princeton University Press.

Andrada, E., C. Rode & R. Blickhan (2013) Grounded running in quails: Simulations indicate benefits of observed fixed aperture angle between legs before touch-down. Journal of Theoretical Biology. 335: 97–107.

Andrada, E., D. Haase, Y. Sutedja, J. Nyakatura, B. Kilbourne, J. Denzler, M. Fischer & R. Blickhan (2015) Mixed gaits in small avian terrestrial locomotion. Scientific Reports. 5, 13636; doi: 10.1038/srep13636.

Baldwin, L. & G. Teleki (1976) Patterns of gibbon behavior on Hall's island, Bermuda. In: Gibbon and Siamang, Vol. 4, (ed. D. Rumbauch). pp. 21-105. Karger, Basel,

Bertram, J. (2004) New Perspectives on Brachiation Mechanics. Yearbook of Physical Anthropology 47:100–117.

Bertram, J. & Y-H. Chang (2001) Mechanical energy oscillations of two brachiation gaits: measurement and simulation. American Journal of Physical Anthropology. 115: 319–326.

Bertram, J., A. Ruina, C. Cannon, Y-H, Chang & M. Colema n (1999). A point-mass model of gibbon locomotion. Journal of Experimental Biology. 202: 2609–2617.

Bertram, J. (2016) Understanding mammalian locomotion. Concepts and applications. John Wiley & Sons.

Bramble D. & D. Liebermann (2004) Endurance running and the evolution of Homo. Nature. 432: 345-352.

Cartmill, M. & K. Milton (1977) The lorisform wrist joint and the evolution of “brachiating” adaptations in the hominoidea. American Journal of Physical Anthropology. 47: 249-279.

Chang, Y-H., J. Bertram & A. Ruina (1997) A dynamic force and moment analysis system for brachiation. Journal of Experimental Biology. 200: 3013–3020.

Chang, Y-H., J. Bertram & D. Lee (2000) External Forces and Torques Generated by the Brachiating White-Handed Gibbon (*Hylobates lar*). American Journal of Physical Anthropology. 113:201–216

Channon, A., M. Günther, R. Crompton & E. Vereecke (2009) Mechanical constraints on the functional morphology of the gibbon hind limb. Journal of Anatomy. 215: 383–400.

Channon, A., R. Crompton, M. Günther, K. D'Août, E. Vereecke (2010a) The Biomechanics of Leaping in Gibbons. American Journal of Physical Anthropology. 143: 403–416.

Channon, A., M. Günther, R. Crompton & E. Vereecke (2010b) Muscle moment arms of the gibbon hind limb: implications for hylobatid locomotion. Journal of Anatomy. 216: 446–462.

Channon A., M. Günther, R. Crompton, K. D'Août, H. Preuschoft & E. Vereecke (2011a) The effect of substrate compliance on the biomechanics of gibbon leaps. Journal of Experimental Biology. 214: 687-696.

Channon, A., J. Usherwood, R. Crompton, M. Günther & E. Vereecke (2011b) The extraordinary athletic performance of leaping gibbons. Biology Letters. doi:10.1098/rsbl.2011.0574.

Fiers, P., D. De Clercq, V. Segers & P. Aerts (2013) Biomechanics of human bipedal gallop: asymmetry dictates leg function. Jounral of Experimental Biology. 216: 1338-1349.

Fleagle, J. (1976) Locomotion and posture of the Malayan siamang and implications for hominid evolution. Folia Primatologica. 26: 245–269.

Fletcher J & B. MacIntosh (2015) Achilles tendon strain energy in distance running: consider the muscle energy cost. Journal of Applied Physiology. 118: 193-199.

Frey, H. (1913) Der Musculus Triceps Surae in der Primatenreiche. Morphologische. Jahrbuch,, 47 : 1-191.

Full, R. & D. Koditscheck (1999) Templates and anchors: neuromechanical hypotheses of legged locomotion on land. Journal of Experimental Biology. 202: 3325–3332.

Geyer, H., A. Seyfarth & R. Blickan (2006) Compliant leg behaviour explains basic dynamics of walking and running. Proceedings of the Royal Society (London),B. 273: 2861-2867.

Gittins, S. (1983) Use of the forest canopy by the agile gibbon. Folia Primatologica. 40: 134–144.

Hannah, J. a D. Schmitt (2011) Interpreting the Role of Climbing in Primate Locomotor Evolution: Are the Biomechanics of Climbing Influenced by Habitual Substrate Use and Anatomy? International Journal of Primatology, 32 : 430-444.

Hof, A., J. Van Zandwijk & M. Bobbert (2002) Mechanics of human triceps surae muscle in walking, running and jumping. Acta Physiologica Scandinavica. 174: 17-30.

Hunt, K. (2016) Why are there apes? Evidence for the co-evolution of ape and monkey ecomorphology. Journal of Anatomy. 228: 630–685.

Ker, R., M. Bennett, S. Bibby, R. Kester & R.McN. Alexander (1987) The spring in the arch of the human foot. Nature. 325: 147-149.

Lai, A., A. Schache, Y, Lin & Marcus G. Pandy (2014) Tendon elastic strain energy in the human ankle plantar-flexors and its role with increased running speed. Journal of Experimental Biology. 217: 3159-3168.

Leardini, A. & J. O'Connor (2002) A model for lever-arm length calculation of the flexor and extensor muscles at the ankle. Gait a Posture. 15: 220-229.

Lichtwark, G. & A. Wilson (2005) In vivo mechanical properties of the human Achilles tendon during one-legged hopping. Journal of Experimental Biology: 208: 4715-4725.

Lichtwark, G. & A. Wilson (2006) Interactions between the human gastrocnemius muscle and the Achilles tendon during incline, level and decline locomotion. Journal of Experimental Biology. 209: 4379-4388.

Lieberman, D (2012) Those feet in ancient times. Nature. 483: 550-551.

Lovejoy C., B. Latimer, G. Suwa, B. Asfaw & T. White (2009a) Combining Prehension and Propulsion: The Foot of Ardipithecus ramidus. Science. 326: 72e1-72e8.

Lovejoy C., G. Suwa, S. Simpson, J. Matternes & T. White (2009b) The Great Divides: Ardipithecus ramidus Reveals the Postcrania of Our Last Common Ancestors with African Apes. Science. 326: 100-106.

Maganaris, C., V. Baltzopoulos & A. Sargeant (2000) In vivo measurements-based estimations of the human Achilles tendon moment arm. European Journal of Applied Physiology. 83: 363-369.

Michilsens, F., K. D'Août & P. Aerts (2011) How Pendulum-Like Are Siamangs? Energy Exchange During Brachiation. American Journal of Physical Anthropology. 154: 581-591.

Michilsens, F. K. D'Août, E. Vereecke & P. Aerts (2012) One step beyond: Different step-to-step transitions exist during continuous contact brachiation in siamangs. Open Biology. doi: 10.1242/bio.2012588

Marsh, R., D. Ellerby, J. Carr, H. Henry & C. Buchanan (2004) Partitioning the Energetics of Walking and Running: Swinging the Limbs Is Expensive. Science. 303: 80-83.

Myatt,J., R. Crompton & S. Thorpe (2011) Hindlimb muscle architecture in non-human great apes and a comparison of methods for analysing inter-species variation. Journal of Anatomy. 219: 150-166.

Preuschoft, H. & B. Demes (1984) Biomechanics of brachiation. In The Lesser Apes: Evolutionary And Behavioral Biology (eds.: H. Preuschoft, D. J. Chivers, W. Y. Brockelman & N. Creel). pp. 96-118. Edinburgh University Press.

Preuschoft H., H. Witte & B. Demes (1992) Biomechanical factors that influence overall body shape of large apes and humans. In: Topics in Primatology, Vol. 3 Evolutionary Biology, Reproductive Endocrinology and Virology (eds Matano S, Tuttle RH, Ishida H, Goodman M), pp. 259–289. University of Tokyo Press.

Sati, J. & J. Alfred (2002) Locomotion and posture in Hoolock gibbon. Ann. For. 10: 298-306.

Standring, S. (2016) Gray's Anatomy: The Anatomical Basis of Clinical Practice (ed. 41). Elsevier.

Swindler, D. & C. Wood (1973) An atlas of primate gross anatomy. Baboon, chimpanzee and men. University of Washington Press.

Thorpe, S. & R. Crompton (2006) Orangutan Positional Behavior and the Nature of Arboreal Locomotion in Hominoidea. American Journal of Physical Anthropology. 131: 384–401.

Thorpe, S., Crompton, R., Günther, M., Ker, R. & Alexander, R.McN. (1999) Dimensions and Moment Arms of the Hind- and Forelimb Muscles of Common Chimpanzees (Pan troglodytes). American Journal of Physical Anthropology. 110: 176-199.

Thorpe S, R. Holder & R. Crompton (2007) Origin of human bipedalism as an adaptation for locomotion on flexible branches. Science. 316: 1328–1331.

389 Uchida, T., J. Hicks, C. Dembia, & S. Delp (2016) Stretching your energetic budget: how tendon
390 compliance affects the metabolic cost of running. PloseOne. DOI:10.1371/journal.pone.0150378.: 1-
391 19.

392 Usherwood, J. & J. Bertram (2003) Understanding brachiation: insight from a collisional perspective.
393 Journal of Experimental Biology. 206: 1631-1642.

394 Usherwood, J., S. Larson & J. Bertram (2003) Mechanisms of Force and Power Production in
395 Unsteady Ricochetal Brachiation. American Journal of Physical Anthropology. 120: 364–372

396 Vereecke, E. & P. Aerts (2008) The mechanics of the gibbon foot and its potential for elastic energy
397 storage during bipedalism. Journal of Experimental Biology. 211: 3661-3670.

398 Vereecke, E. & A. Channon (2013) The role of hind limb tendons in gibbon locomotion: springs or
399 strings? Journal of Experimental Biology. 216: 3971-3980.

400 Vereecke, E., K. D'Août,, R. Payne & P. Aerts (2005a) Functional analysis of the foot and ankle
401 myology of gibbons and bonobos. Journal of Anatomy. 206: 453-476.

402 Vereecke, E., K. D'Août, L. Van Elsacker & P. Aerts (2005b) Functional Analysis of the Gibbon Foot
403 During Terrestrial Bipedal Walking: Plantar Pressure Distributions and Three-Dimensional Ground
404 Reaction Forces. American Journal of Physical Anthropology. 128: 659-669.

405 Vereecke, E., K. D'Août, & P. Aerts (2006a) Locomotor versatility in the white-handed gibbon
406 (Hylobates lar): A spatiotemporal analysis of the bipedal, tripedal, and quadrupedal gaits. Journal of
407 Human Evoluition. 50: 552-567.

408 Vereecke, E., K. D'Août, & P. Aerts (2006b) The dynamics of hylobatid bipedalism: evidence for an
409 energy-saving mechanism? Journal of Experimental Biology. 209: 2829-2838.

410 Vereecke, E., K. D'Août, & P. Aerts (2006c) Speed modulation in hylobatid bipedalism: A kinematic
411 analysis. Journal of Human Evolution. 51: 513-526.

412 Willems, P., G. Cavagna & N. Heglund (1995) External, internal and total work in human locomotion.
413 Journal of Experimental Biology. 198: 379-393.

414 Woledge, R., N. Curtin & E. Homsher (1985) Energetic aspects of Muscle contraction. Academic Press.

415

416

417

418

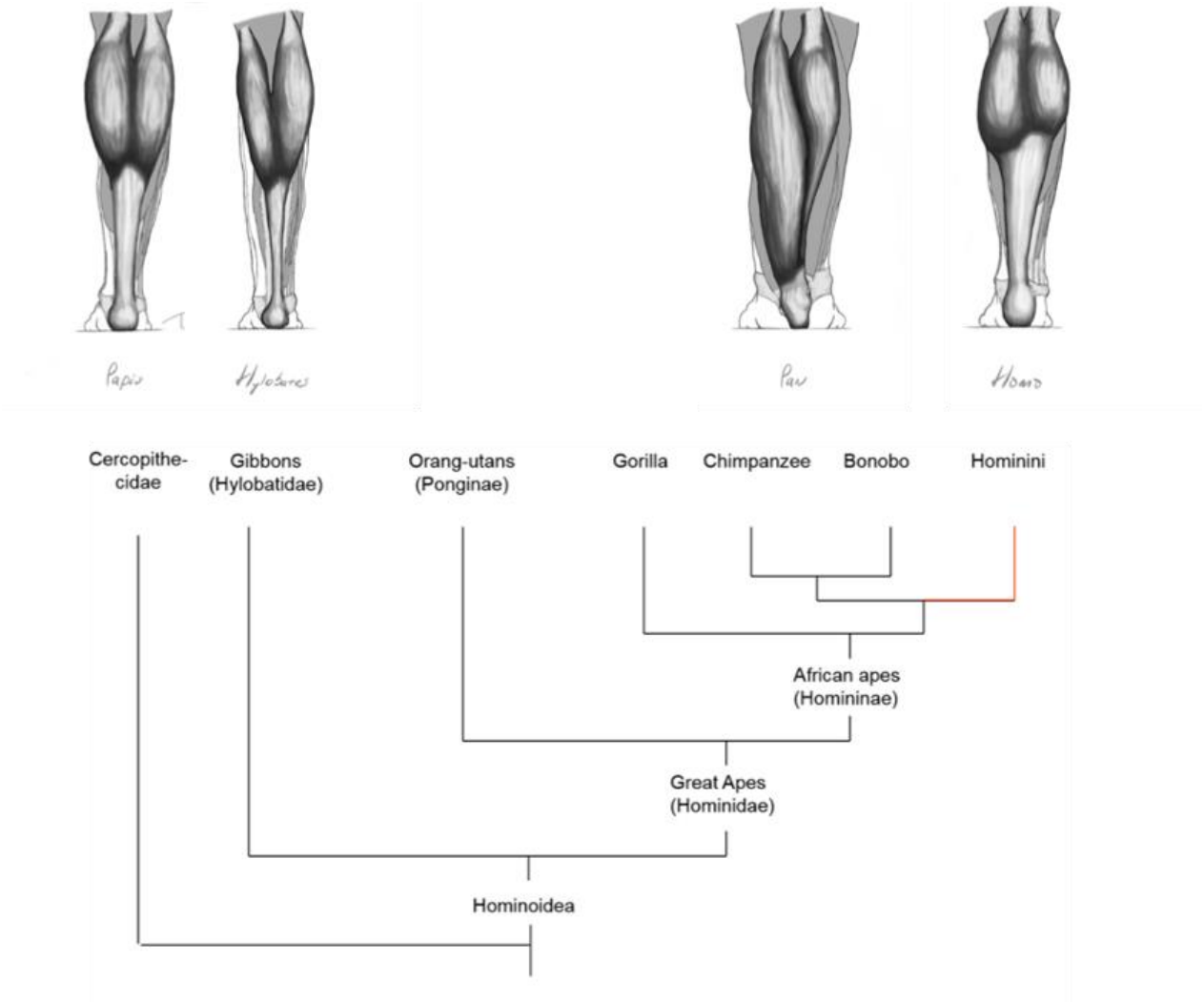

Figure 1 : Phylogenetic tree of the Catarrhini, with dorsal views of the baboon, gibbon, chimpanzee and human lower leg showing the Achilles tendon and the gastrocnemius muscle (anatomical drawings: courtesy of Timo Van Leeuwen).

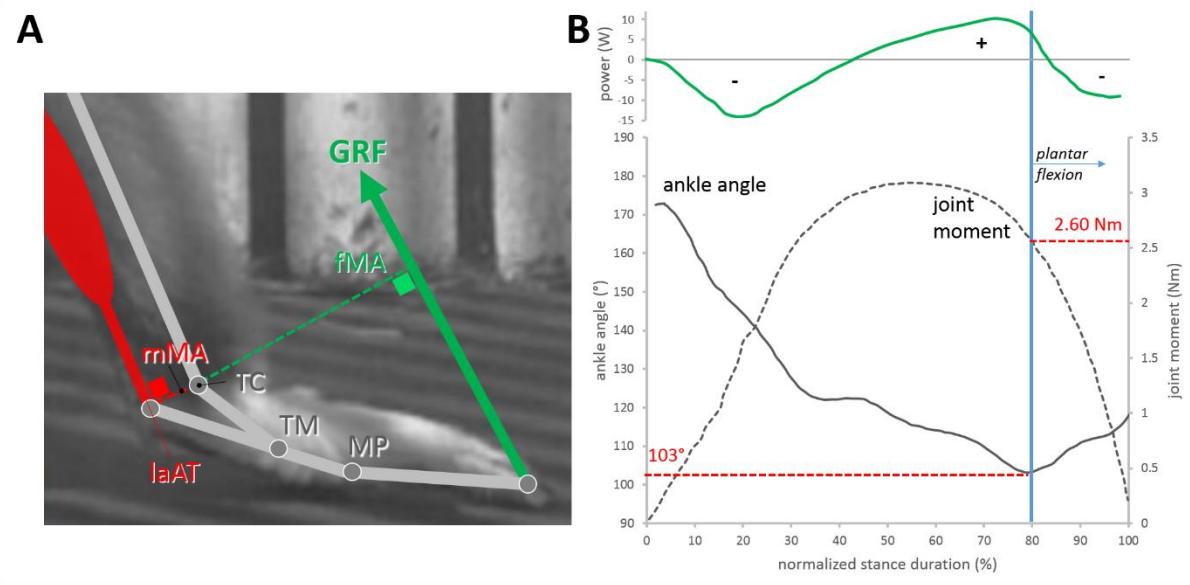

Figure 2 A: Schematic representation of the lower leg and foot of the white-handed gibbon (dark grey sticks) at the instant of initial foot contact during bipedal 'grounded' running (background: still frame of a video sequence). The ankle (talocrural) (TC), tarsometatarsal (TM) and metatarsophalangeal (MP) joints are shown. The moment arm (fMA) of the ground reaction force (GRF, green arrow) and the moment arm (mMA) of the balancing force acting along the Achilles tendon, both with respect to the ankle joint, are indicated. The triceps surae and its Achilles tendon are schematically represented in red. The fMA is the perpendicular distance from the TC to the GRF; the mMA from the TC to the line of action of the Achilles Tendon (laAT). B: *Upper panel*; instantaneous mechanical power of the BCOM during stance. When positive, energy is being added to the BCOM. When negative, BCOM energy dissipates. The vertical blue line indicates the instant of transition from ankle dorsi-flexion to ankle plantar-flexion (= extension of the ankle joint). For the largest part, plantar flexion (recoil eventually adding energy) occurs when, overall, whole-body energy decreases (see text). *Lower panel*; average ankle joint angle (solid curve; left vertical axis) and average joint moment of the GRF at TC (dashed curve; right vertical axis) are given as a function of normalized stance time (0% = initial foot contact; 100% = toe off) in the white-handed gibbon. This plantar flexion represents the foot push-off which can partially be powered by the release of strain energy stored in the Achilles tendon. At this transition, the ankle joint angle equals 103°, while the according joint moment is 2.60 Nm (for more explanation: see text). (Based on Vereecke and Aerts, 2008; see also Supplementary Material for more details in methods).